

A NEW SUBGENUS AND TWO NEW SPECIES OF THE  
GENUS *MACHILINUS* (MEINERTELLIDAE,  
ARCHAEOGNATHA = MICROCORYPHIA, "APTERYGOTA",  
INSECTA) FROM MEXICO

HELMUT STURM

Department of Biology, University of Hildesheim, D-31141 Hildesheim, Germany

*Abstract.*—*Protomachilinus* NEW SUBGENUS, *M. (P.) mexicanus* NEW SPECIES and *M. (P.) oaxacensis* NEW SPECIES are described. The new subgenus is more plesiomorphic than any of the other three subgenera of *Machilinus*. Ecological and biogeographical aspects of the genus are discussed.

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The genus *Machilinus* has a special position within the Meinertellidae, a family which is more derived than the other family of extant Archaeognatha, the Machilidae. There are three reasons for this. From the morphological point of view the *Machilinus* species described up until now are highly derived, e.g. by sublateral ocelli which are round to elliptical and hyaline to light red; the absence of a horizontal process on the base of the maxillary palp (a process which is present in all other genera of Meinertellidae); the absence of coxal stylets on all legs; the absence of coxal vesicles on abdominal coxosternite I and the highly reduced chaetotaxy on gonapophyses VIII and IX of the females (Sturm and Bach, 1993).

The ecology of this taxon also shows some peculiarities. Contrasting with nearly all other genera most *Machilinus* species are active during full daylight (The only other species for which daylight activity is described is *Bachilis multisetosa* of the family Machilidae: Mendes, 1977). Some species were found in very dry localities and one species collected at 4500 m above sea level, near Tucuman, Argentina (Wygodzinsky, 1967). Noteworthy is also the biogeographical aspect. The species of the genus described since then were collected in the western part of North America, the southern part of South America, the mediterranean area, the middle of the Sahara and in South Africa. As a result *Machilinus* is second only to the genus *Machiloides* (Meinertellidae) in being the most widespread genus of the Archaeognatha (Wygodzinsky, 1967 Sturm, 1984).

The present work reports a new subgenus from Mexico. This finding takes on added importance by the fact that this subgenus shows several plesiomorphic characters and is doubtless the most primitive of the four subgenera of *Machilinus*. Some of its characteristics establish a connection between the genus *Machilinus* fairly isolated before and the other genera of the Meinertellidae. These characters also make it necessary to redescribe some generotypic features. As a result of the discovery of the new subgenus in Mexico questions arise about biogeography and evolution of the genus, discussed after the description.

**Protomachilinus** Sturm, New Subgenus

Type species: *Machilinus (P.) mexicanus*, new species

**Diagnosis:** As subgenus *Machilinus* s.str. except: Lateral ocelli big, elliptic, with

black pigment situated on an indentation of the ventral margin of the eyes; 4 distal teeth of mandible without distinct pigment.—Maxillary palps: Horizontal projection on the dorsal basis present; article 2 of male without distinct specializations referring to form and chaetotaxy.—Labial palps: Article 3 distinctly broadened, in males more than in females.—Abdomen: Sternocoxites I with 1 + 1 functioning coxal vesicles. **Etymology:** The subgenus is named after the accumulation of plesiomorphic characters: protos (Greek) = first (in the sense of original).

**Discussion:** The combination of characteristics mentioned above distinguish the subgenus from the 3 other subgenera of the genus. They are (with exception of the broadened article 3 of labial palps) plesiomorphic and are present either in all other genera of Meinertellidae (horizontal process on the basis of maxillary palps) or the majority of the taxa (lateral ocelli with distinct black pigment, teeth of mandible without pigment, coxal vesicles on sternocoxite I present). Certainly the interrupted pattern of macrochaetae on gonapophyses VIII and IX of female (ovipositor-type IV after Sturm and Bach, 1993) is present but it is more weakly developed than in the other 3 subgenera (see Figs. 25, 26).

On the other hand in view of the number of differences with the other subgenera the question arises if this taxon could should actually be a genus. The main reason against this possibility are the many derived common characteristics, shared with the other subgenera of the genus *Machilinus* (Sturm and Bach, 1992), e.g. sublateral position of lateral ocelli and their ovoid or elliptical form, size and form of eyes, similar distribution of spiniform setae on the margins of thoracic tergites I–III (Sturm and Messner, 1995); absence of coxal stylets on legs, presence of characteristic setae near the basis of abdominal stylets; penis with thin straight setae on characteristic bumps; derived chaetotaxy of female gonapophyses.

### ***Machilinus* (*Protomachilinus*) *mexicanus* Sturm, New Species**

**Types:** Holotype male, body length 7.5 mm; MEXICO, Chiapas, 5 mi W San Cristobal, pine-oak-forest, 24.VIII.1966, J. & W. Ivie coll.—Allotype female, 8.5 mm, same data as type. Paratypes: 1 female 9.5 mm; 1 juvenile 4.5 mm, same data as type. All specimens deposited in AMNH (3 adult specimens prepared on slides: Euparal inclusion).

**Etymology:** the species is named after the country of origin, Mexico.

**Description:** Body length ca. 7–10 mm; hypodermal pigment dark brown, extended especially on head, mandibles, maxillary palps, labium, legs and thoracic sternites (see Figs. 1, 4, 6–9).

**Head** (Fig. 1): Eyes large; ratio of width of eyes : width of head = 0.75–0.83; length of eyes : width ca. 0.8; line of contact of the eyes : length of eyes = 0.6–0.7.—Paired ocelli sublateral; contrasting with the other subgenera by black pigment and great size; width reaching nearly half width of eyes.—Antennae (Figs. 2, 3) shorter than body, up to 6.5 mm long, with weak and uniform light brown pigmentation; scapus short, ratio length to width = 1.5–1.9, distal chains of the flagellum with up to 11 articles, obviously limited by jointlets.—Mandibles distally with 4 teeth of equal size, without distinct pigmentation.—Maxillary palps (Figs. 4, 5): On the dorsal base a horizontal process is present; such a process is absent in all other subgenera of *Machilinus* but present in all other Meinertellidae; hook on article 2 of male and

chaetotaxy on articles 2 + 3 without distinct peculiarities; number of spines on articles 7/ 6/ 5 = ca. 10/ 13/ 3; ratio length of articles 7:6:5:4:3 = 1:1.7–2:1.85–2.05:1–1.1:0.9–1 (for the 2 females), articles 4–7 in the male absent (broken).—Labium (Figs. 6, 7): Article 3 of palps distally distinctly broadened, in the male more than in the female.

*Thorax*: Number of lateral marginal spiniform setae on tergites I/II/III = 12–15/35–47/10–16 (cf. Sturm and Messner, 1995).—Legs (Figs. 8, 9): Coxal stylets absent; some dark spiniform setae on tarsal articles 1 + 2 of legs I.

*Abdomen*: Coxites I–VII each with 1 + 1 functioning coxal vesicles, II–IX with stylets; all sternites small, terminal spines of stylets long (Figs. 12, 13), ratio length of terminal spine: length of stylet for segments II = 0.4–0.5:1 for V = 0.8–1.0:1; for IX = 0.6–0.65:1 (determined only in male); distance between inner margins of basis of abdominal stylets only slightly different, ratio of distance segment IV:II = 1.2–1.35 (cf. description of the other subgenera in Sturm and Bach, 1992); coxites II + III with small fields of setae lateral to the base of stylets, setae up to ca. 0.15 mm long, straight and of brown colour (Fig. 11); stylets IX ventrad and mediad with brown spiniform setae, up to 0.45 mm long (Fig. 13).—Penis (Fig. 14): distinctly shorter than  $0.5 \times$  length of coxite IX; aperture pointed oval, surrounded by 1–3 rows of straight setae (up to 0.03 mm long) rising on small characteristic bumps. Ovipositor extended far beyond terminal spines of stylets IX; gonapophyses with more than 60 articles, only on the distal third with macrochaetae; terminal spine of middle size, reaching the length of 2–3 terminal articles; 3–5 setae per article on the four most distal articles, proximally reduced to 1–3; lateral macrochaetae in this latter area not present on each article (interrupted pattern of distribution after Sturm and Bach 1993).—Cerci with long straight terminal spines (Fig. 18).

**Diagnosis:** The species can be determined by the characteristics of the subgenus and the differences which are given in the diagnosis of *Machilinus (P.) oaxacensis*.

### ***Machilinus (Protomachilinus) oaxacensis* Sturm, New Species**

**Types:** Holotype male, body length 6.5 mm; MEXICO, Oaxaca county, near Tlacolula, 96.27 W, 16.57 N, under cliff, 30.IV.1963, Gertsch & Ivie coll.—Allotype: female, body length 7 mm, same data as holotype; paratypes 1 male, 4 females, same data as holotype.—Paratypes: 2 females, 6.5 and 8 mm; MEXICO, Oaxaca, 3 mi SE Tlacolula 96.25 W, 16.56 N, 30 VIII. 1966, J.& W. Ivie coll.—All types deposited on AMNH, 6 adult specimens prepared on slides (Euparal inclusion).

**Etymology:** The species name refers to the province Oaxaca (Mexico) where the species was collected.

**Description:** Body length (inclusive of head) ca. 6–8 mm; hypodermal pigment dark brown, more pronounced than in the first species.

*Head:* Hypodermal pigment on frons V-shaped, with small median stripe (Fig. 19).—Ratio of width of eyes: width of head = 0.75–0.85; length of eyes: width = 0.75–0.9; length line of contact of eyes: length of eyes = 0.55–0.65; width of ocelli: width of eyes = 0.45–0.55 ( $n = 6$  for all values); ocelli black. Antennae distinctly shorter than the body, maximum length measured = 3.5 mm; maximum number of articles per chain within the distal half = 9; patches of hypodermal pigment on scapus and pedicellus only; flagellum uniformly light brown; scapus short, ratio length: width

= 1.5–1.9—Maxillary palps especially on article 3 stronger pigmented than in the first species; setae on the medial side of article 2 forming an indistinct whorl (Fig. 20); ratio length of articles 7:6:5:4:3 = 1:1.4–1.6:1.7–2.3:1.1–1.3:1.1–1.5 (n = 12); number of spines on articles 7/6/5 = 5–7/9–11/1–2.—Broadening on article 3 of labial palp of female weak, of male very distinctive.

*Thorax:* Legs more intensive and more extended pigmented than in the first species; spiniform setae on all legs present (Fig. 22); maximum numbers on femur/tibia/tarsus 1/tarsus 2 for leg I = –/3/3/5; for II = 2/5/4/4; for III = 3/5/4/4. Maximum number of lateral marginal setae on tergites I/II/III = 19 (partially in double rows)/>50/16.—All sternites with big patches of hypodermal pigment.

*Abdomen:* Coxal vesicles on coxites I–VII; stylets on II–IX; coxites I with a small band of setae on the anterior border (Fig. 23); fields of setae near the base of stylets on coxites II–VIII present; terminal spines on stylets long; ratio of length of spine : length of stylet on segment II ca. 0.5, on V ca. 0.5–0.6, on IX ca. 0.35–0.45. Penis: Aperture great, pointed triangular; structure and taxis of setae similar to those of the first species. Ovipositor thin, extended well past the ends of terminal spines IX; chaetotaxy similar to the first species. Filum terminale and cerci with many dark brown spiniform setae; cerci up to 3.3 mm long with one terminal spine of medium size.

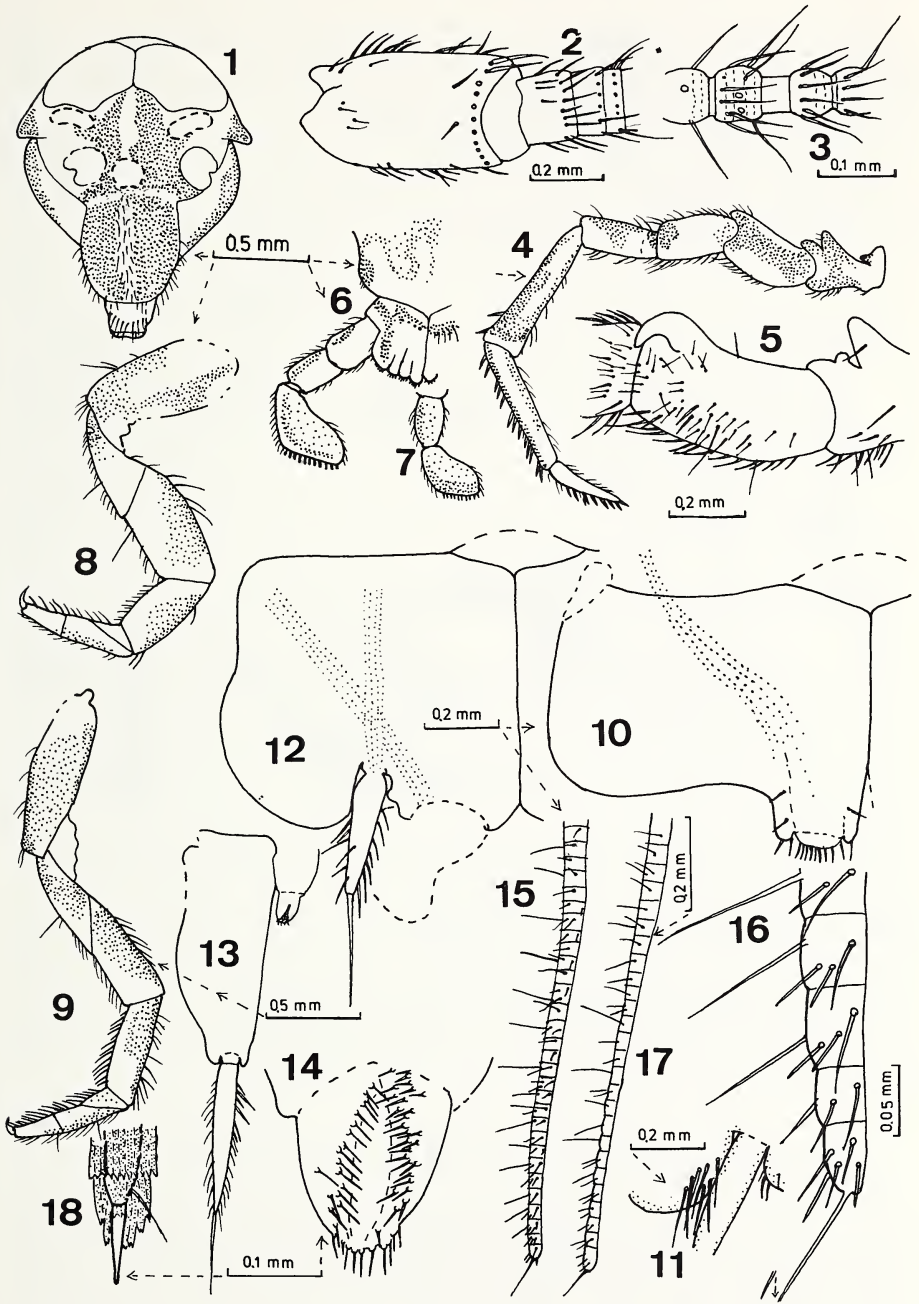
**Diagnosis:** *Machilinus (P.) oaxacensis* is distinguished from the other species of the subgenus e.g. by the shorter body length, the different pigment pattern on the frons and maxillary palps, different ratios of length of articles on maxillary palps, the strong broadening of article 3 on the labial palps of the male, presence of dark spiniform setae on the tibia and tarsus of all legs, and the presence of fields of setae near the bases of stylets II–VIII.

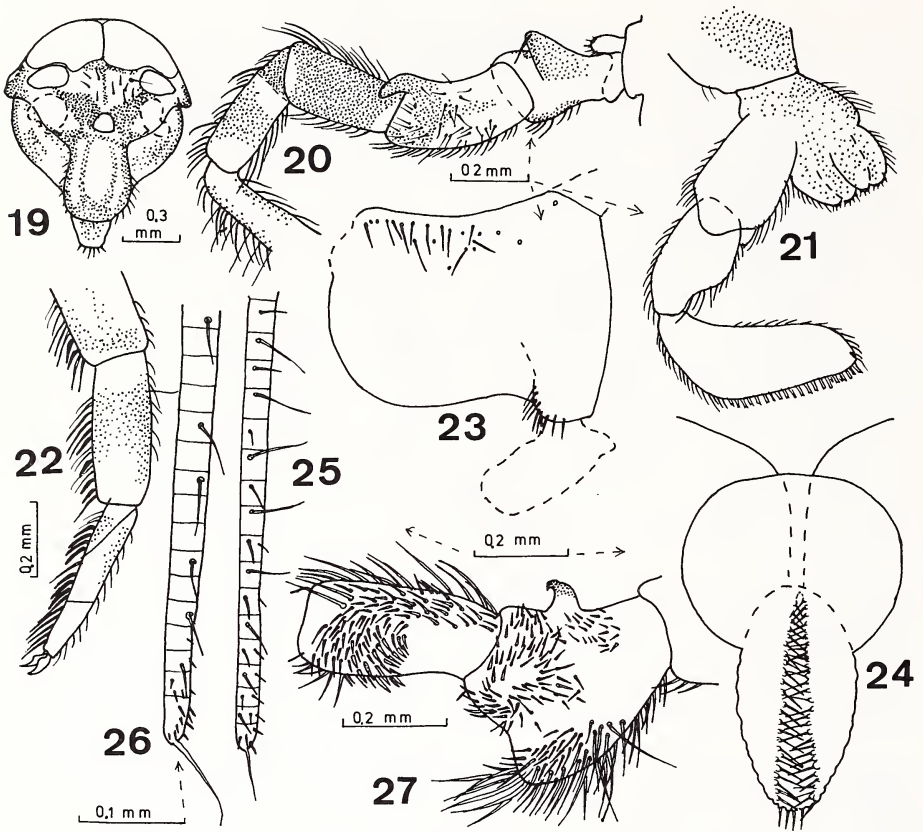
**Discussion:** The species presents all characteristics of the subgenus. Specimens which were collected in 1966 at a locality near the type locality included a female (9 mm body length) with a distinctly different ratio of distances between stylets on segments II and IV (= 1,14) and some other peculiarities. It can not put to this species but indicates that there are probably more species of the subgenus which contrasts with the subgenus *Nearctolinus* with only one species and a much larger distribution.

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Figs. 1–18. *Machilinus (Protomachilinus) mexicanus*, new species. 1. Head (male), frontal view. 2. + 3. Antenna, female; 2. Basal part with scapus + pedicellus; 3. Distal part, ca. 4 mm from base. 4. Maxillary palp (female), lateral view. 5. Articles 1–3 of male maxillary palp, median side, article 2 with hook. 6. Left half of labium with labial palp (male), ventral view. 7. Labial palp (female), articles 2 + 3. 8. Leg I (male). 9. Leg III (male). 10. Half of coxosternite I (male), ventral view. 11. Part of coxite III (male) with base of stylet and lateral setal area, ventral view. 12. Half of coxosternite V (male) with muscles (dotted) and coxal vesicle, ventral view. 13. Coxite IX (male) with penis, ventral view. 14. Penis of Fig. 13 by higher magnification. 15. + 16. Distal parts of gonapophyses VIII (female), ventral view. 17. Distal part of gonapophysis IX (female), ventral view. 18. Distal end of cercus (female) with big terminal spine.







Figs. 19–26. *Machilinus* (*Protomachilinus*) *oaxacensis*, new species; hypodermal pigment dotted. 19. Head (male), frontal view. 20. Maxillary palp (male), articles 1–5, lateral view, inner side. 21. Left half of labium (male) with labial palp, ventral view. 22. Distal part of leg III (male) with spiniform setae. 23. Half of sternocoxite I with coxal vesicle and fields of setae, ventral view. 24. Penis, ventral view. 25. Distal part of gonapophysis IX (female), ventral view. 26. Distal part of gonapophysis IX of *Machilinus* (*Nearctolinus*) *aurantiacus*: Interrupted pattern of macrochaetae more significant than in 25.; ex Sturm and Bach 1992. 27. *Machilinus* (*Neotropolinus*) *chilensis* Sturm and Bach, 1992: Maxillary palp (male), articles 2 + 3: high specialized chaetotaxy and form of article 2; ex Sturm and Bach 1992.

#### ECOLOGICAL AND BIOGEOGRAPHICAL ASPECTS OF THE GENUS *MACHILINUS*

The localities where specimens of the genus were found show very different ecological conditions: rocks or stones of very different composition, sand dunes, bark of fallen trees, litter, heath and grassland. The range of altitude reaches from marine beaches (Mendes, 1977) up to 4500 m above sealevel (Argentina: Wygodzinsky, 1967). Peculiar for Archaeognatha is the activity in full light. It was described by different authors (e.g. Wygodzinsky, 1952, Bitsch, 1968, Smith, 1970, Mendes, 1977) and is probably valid for most of the *Machilinus* species. For nearly all other

genera activity during night or dusk is regular. Only for *Bachilis multisetosa* (Machilidae) Mendes (1977) mentioned a less pronounced daylight activity. Perhaps the light or reddish colour described for the three other subgenera of *Machilinus* and for *Bachilis m.* is connected with this form of activity. The black colour of the paired ocelli in the subgenus *Protomachilinus* corresponds to that of nearly all other Archaeognatha and it remains unclear if it indicates activity in darkness or twilight. The hygrophily is apparently developed differently within the genus. Besides species or populations which are living in habitats with high relative humidity (e.g. *M. chilensis* in the forests of Chile; Sturm and Bach, 1992) or *M. gredosi* in the Serra da Estrela, Portugal, an area with 1900 mm precipitation per year: Mendes 1977) there are some species living in dry areas (e.g., *M. aurantiacus* on the sand dunes near Los Angeles [collected by R. Mattoni, Beverly Hills: VII. + VIII. 1993 in pitfall traps] and on dry localities in Utah and New Mexico (Mendes, 1996) or active for long time in full sunlight. In the latter cases a regular production of dew during the night could stabilize the water balance. But it is an enigma why *M. aurantiacus* often living in dry habitats would have strongly reduced coxal vesicles. For other bristle-tails the uptake of water by means of the coxal vesicles is regular (Bitsch, 1974). It may be that the genus *Machilinus* in connection with the daylight activity has achieved other means of water balance.

The genus *Machilinus* does not enter tropical lowlands. The collecting localities in Mexico are lying at altitudes of more than 1000 m, those at Tibesti Mountains and in Yemen at more than 2000 m.

The geographic distribution of the genus *Machilinus* is characterized by a multitude of isolated and widely distributed areas. Three of these areas are situated in America, each harboring one subgenus. The number of species decreases from South to North with South America having 6, Mexico 2, North America 1 (Fig. 28). The fourth subgenus is restricted to the Western part of the Old World and distributed in at least 4 clearly separated areas (at the basis of the data known at the present time). Old data referring to the occurrence on the Cape Verde Islands (Silvestri, 1908) could not be confirmed. The area with the highest number of species (18) is the Mediterranean. The remaining areas are very small, each harboring 1 species. The occurrences in Tibesti, Yemen and South Africa could be relicts, that in Madeira perhaps a result of dispersal.

Within the four subgenera of *Machilinus*, *Protomachilinus* undoubtedly shows the most plesiomorphic characters, which makes the genus morphologically more similar to the other genera of Meinertellidae.

An undescribed specimen from the Lebanese amber (collection of the American University at Beirut, number 194/35) gives evidence for the existence of typical representatives of the family Meinertellidae some 110–120 millions of years ago. The splitting within this family must have been happened distinctly earlier, perhaps at the beginning of the Mesozoic. An explanation for the present distribution on the basis of the known historical, biogeographic and morphological data remains difficult, but a comparison with the distribution of another taxon of the Meinertellidae, the genus *Machiloides* could be helpful. *Machiloides* is not only the most plesiomorphic genus in the Meinertellidae (e.g. coxal stylets on legs II and III, lateral ocelli sole-shaped, chaetotaxy on genital appendages not specialized) but it shows also the most extensive distribution within the extant Archaeognatha (Table 1).

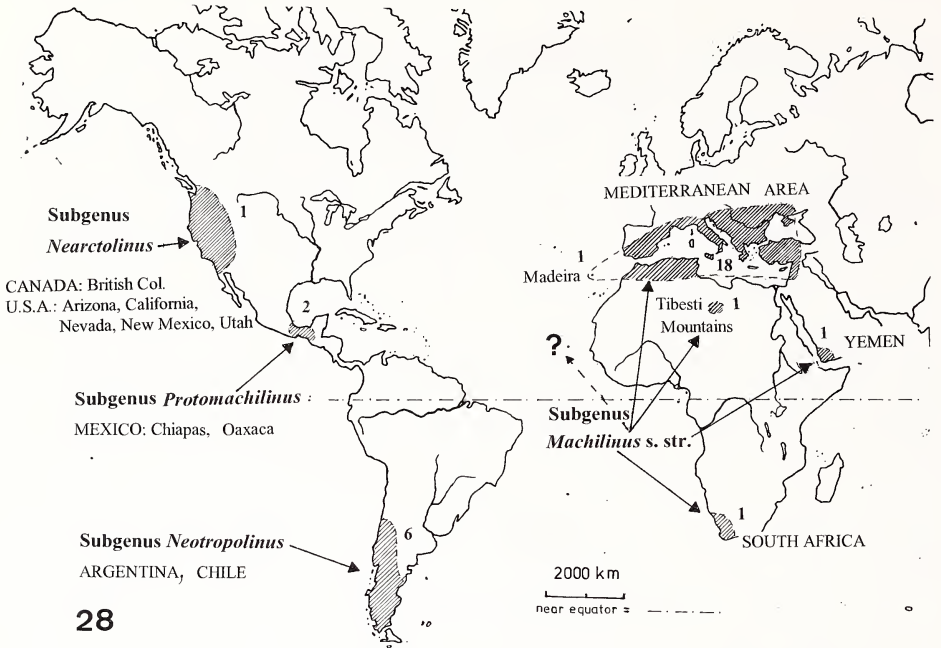


Fig. 28. Geographical distribution of the 4 subgenera of the genus *Machilinus*; areas hatched; numbers = number of species per area; ? = occurrence uncertain.

The fact that no other genus of Archaeognatha shows such an extensive distribution as these two genera suggests the long period of time necessary to reach such a wide distribution and morphological differentiation. Probably the origin of both genera and of all Archaeognatha was in the northern hemisphere, where presently occur the most plesiomorphic species of *Machilinus* and *Machiloides* (*Machilinus* [*Protomachilinus*] in Mexico and *Machiloides tenuicornis* in Spain). If Laurasian in origin, the dispersal of *Machiloides* began earlier than that of the more derived genus *Machilinus*, which apparently never reached the Austral-malesian area. A similar pattern of distribution is in the genus *Araucaria* (Gymnospermae) during the Mesozoic, especially during the Cre-

Table 1. Distribution and number of species for each region for the genera *Machilinus* and *Machiloides* (Meinertellidae).

	<i>Machilinus</i>	<i>Machiloides</i>
North America	1	2
Central America	2	—
South of South America	6	10
South and East Africa	1	25
Mediterranean Region	19	1
Australia/Tasmania	—	>2



taceous period, and included North America, Southern South America, Europe, South Africa, India and the Australian region (Ehrendorfer, 1978).

#### ACKNOWLEDGMENTS

I am indebted to Dr. Randall T. Schuh of the American Museum of Natural History, New York for the loan of this interesting material, to Dr. Grimaldi of the same Museum for the revision of the English text.

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Received 24 February 1997; accepted 5 August 1997.